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Electrical Characteristics of the Electric Tissue of the Electric Eel, *Electrophorus electricus* (Linnaeus).

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&

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(Plate I; Text-figures 1 & 2).

A previous paper[1] by the present authors jointly with L. P. Granath described observations made with a cathode-ray oscillograph of the discharge of the electric eel. In that work two types of discharge, the "major" and "minor," characterized by repeatable peak voltages, were identified as the discharges of the large organs and the organs of Sachs respectively. Other discharges, of indefinite peak voltage but identified by their occurrence only between a minor and an ensuing train of major discharges, were assigned to a third type under the name "intermediate," and were tentatively associated with the organs of Hunter. Observations made with external electrodes on the skin of the eel out of water showed that the major discharge runs along the large organ as a pulse of potential gradient at a speed of the order of 500 to 1,000 meters per second.

On the completion of this part of the work it was considered advisable to carry the research for a time to a place where the electric eel was plentiful and could be observed in the wild state or at least under nearly natural conditions. Accordingly an expedition was organized by New York University and the New York Aquarium. Its expenses were met by a generous grant from the Doctor Simon Baruch Foundation, for which we wish to express our gratitude. To the Goeldi Museum of Para, Brazil, we are indebted for a laboratory and facilities for the work, and to Dr. Hagmann and Snhr. Pira of the staff of the Museum we are particularly obliged for their constant kind assistance. Specimens for observation were supplied by Mr. Karl Griem. He and his associates, Messrs. Hory, and Weber, were most helpful. We should like to give our thanks also to the Brazilian Embassy in Washington, to Mr. George E. Seltzer and Mr. Reginald S. Kazanjian of the U. S. Consulate at Para, and to Dr. Eladio da Cruz Lima and a number of other residents of Para for facilitating arrangements for the expedition. To Mr. Robert S. Mathews and Miss Shelby Shackelford, members of the expedition, we are indebted for a great deal of varied assistance.

The observations made at the Goeldi Museum confirmed in general and extended those made earlier in New York. A report of them has been published in abstract.[2] In the present paper some of these observations are combined with others made later at the New York Aquarium. Whereas our first observations at the Aquarium were almost wholly concerned with the variation in the external voltage along the electric organs at different instants during the discharge, the present work undertakes to determine some of the electrical characteristics of the electric tissue and to make some inferences concerning the process of electric discharge.

It has long been surmised that the electric organ of electric fish is in some sort a battery of cells. Thus Faraday remarked of the torpedo:

"In concluding this summary of the powers of torpedinal electricity, I cannot refrain from pointing out the enormous absolute quantity of electricity which the animal must put in circulation at each effort. . . . These circumstances indicate that the torpedo has power (in the way probably that Cavendish describes) to continue the evolution for a sensible time, so that its successive discharges rather resemble those of a voltaic arrangement, intermitting in its action, than those of a Leyden apparatus, charged and discharged many times in succession."[3]

There is a variety of other evidence pointing to the same conclusion. The possibility of generation of electromotive force by the conversion of mechanical energy, as in an electrostatic or an electromagnetic generator, is precluded by the absence of any structure in the organ suitable to this conversion and by the observation that no muscular action is required for the discharge. The possibility that the discharge is generated by the thermoelectric effect is similarly ruled out by the lack of suitable structure and of the requisite differences in temperature.

There remain to be considered only electrochemical processes, and their consideration here is rendered reasonable by the fact that the minute electrical effects observed in nerve and muscle tissue have been convincingly ascribed by recent research to such processes. The voltages observed in nerves and muscles have been identified as concentration potentials. The theory of their production is that the cell membrane is permeable to one ion of an electrolyte and impermeable to the other ion. If then the electrolyte is present in different concentrations on the two sides of the membrane, there will be a migration through the cell membrane of the ions to which it is permeable. The region on the side of lower concentration will thus acquire an electric charge of the sign of these ions and an equal charge of the opposite sign will be left on the other side. The ions which pass through the membrane will hinder the migration of other like ions by the electrostatic repulsion they exert on charges of their own sign, and in time an equilibrium will be reached characterized by a definite voltage across the membrane. This voltage is determined by the chemical valence of the diffusing ion, by the relative concentrations of the electrolyte on the two sides of the membrane, and by the temperature. These conditions being known, the voltage is calculable. In the case of the boundary of a nerve fiber, the relative concentration of potassium on the inside and outside of the fiber, as found by Fenn, Cobb, Hegnauer and Marsh,[4] would give rise at room temperature to a concentration voltage of 118 millivolts. This is much greater than the voltages actually observed in experiments with nerve, but the means of observation are not such as to reveal the maximum voltage.

The voltages observed in the discharge of the electric eel, on the other hand, are very much greater than the concentration voltage found across any single membrane. We have observed voltages as high as 500 between the anterior and posterior ends of the large electric organ, and voltages

[2] Cox, R. T. & R. S. Mathews. *Journal of Applied Physics,* Feb., 1938. (Abstract).

[3] Experimental Researches in Electricity. Everyman's Library Edition, London, 1922. Page 26.

[4] Cited by Erlanger & Gasser. Electrical Signs of Nervous Activity, Philadelphia, 1937. Page 134.

above 300 are common. Such voltages as these must be the sums of many concentration voltages. Each unit or electroplax of the electric tissue is divided by a vertical partition, and we suppose this partition is the boundary across which the concentration voltage is developed, so that each electroplax is a single concentration cell. E. du Bois-Reymond[5] gives the dimension of one electroplax of the large organ in the direction in which the electric polarity is developed as 0.1 mm., so that there would be about 100 cells to the centimeter. If the cells in line along the organ are all joined in series, the electromotive force (which is the voltage measured when no appreciable current is flowing) of the whole series is the sum of the electromotive forces of the separate cells. With 100 cells to the centimeter and 100 millivolts to the cell, an electromotive force of 10 volts would be developed in one centimeter. This is approximately what we measure near the anterior end of the large organs.

It seems then altogether probable that the electromotive force of the electric organs is that of a series of cells, in each of which there is developed a concentration voltage by the selective diffusion of ions through a boundary. The cells in any cross-section of the electric organ we suppose act in parallel. The electromotive force is not thereby increased, since a number of similar cells in parallel have only the electromotive force of each one of them. But when a parallel array of cells is joined to an external conductor, so that a circuit is made and a current flows, the total current in the external conductor is the sum of the currents in the cells. Thus we suppose that the parallel action of the cells of the electric organ serves to produce the large currents (of the order of one ampere at maximum) which we have observed.

We have now to account for the release of energy by the electric organ in brief transient discharges. Evidently the electromotive forces of the cells and their connection in series cannot both be maintained all the time, for if it were so, there would not be transient discharges, but at all times an electric current would flow in the water around the fish. Hence either the electromotive forces of the cells, or their connection in series, or possibly both, must be transient, existing only for the duration of the discharge.

The structure of the electric tissue seems adapted to a transient series connection rather than to a transient generation of electromotive force. The discharge at any part of the organ is evidently governed by the nerve branching to that part, for transsection of the nerve cord stops the progress of the discharge down the organ at the point of transsection. On the other hand, transsection of the electric organ without injury to the nerve cord makes no appreciable difference in either the open circuit voltage or the rate of propagation of the discharge. There is an ending of a nerve fiber on the posterior face of each cell of the electric tissue. A fall of the resistance of the sheath of a nerve fiber during the nervous impulse is well established. It seems reasonable to suppose that, except during the discharge of the organ, cells adjacent along its axis are effectively insulated from each other by the high resistance of the nerve sheath, but when a nervous impulse reaches the end of a fiber the drop in this resistance makes an electrical connection between the posterior (electrically negative) face of each cell and the anterior (electrically positive) face of the cell next behind, so that there follows a progressive connection in series of the cells all along the organ.

Several observations on the discharge give qualitative evidence that the discharge is produced by a transient connection in series of cells with constant electromotive force rather than by the transient generation of electromotive force in cells permanently connected in series. If two points on the large organ are connected to the oscillograph with the circuit open,

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[5] du Bois-Reymond, Emil. Dr. Carl Sachs Untersuchungen am Zitteraal *Gymnotus electricus*, Leipsig, 1881. Page 49.

so that no current flows except that which makes a circuit within the tissue of the eel, one of the most striking features of the oscillographic trace is the uniformity of the peak voltage throughout a long series of discharges. In this case, since the current flowing in the electric tissue must be rather small, the observed peak voltage must be near the full electromotive force. Thus it appears that the electromotive force, at least at the peak, is nearly the same in successive discharges. But when a circuit is made through the organ and an external conductor of low resistance, so that a large current flows, the peak voltages are observed to be less uniform. In this case, the peak voltage is the electromotive force less the drop in voltage caused by the dissipation of energy in maintaining a current through the internal resistance of the tissue. It appears then that, while the electromotive force is nearly uniform at the peaks of successive discharges, the internal resistance is somewhat variable. This would seem to lend some support to the hypothesis that the electromotive force is uniform not only at the peaks of discharges but also during and between them, the discharge being produced by a variation in the internal resistance such as would occur in the transient series connection of the cells.

Another evidence, more convincing than this, is obtained when the oscillograph is connected to two points near the posterior end of the large organ and the two ends of the whole organ are short-circuited by a low resistance. The voltage recorded by the oscillograph is the electromotive force of the segment included between the points of contact less the drop in voltage caused by the current which the electromotive force of the entire organ sends through this segment. The electromotive force of this segment alone would make the anterior end of the segment positive with respect to the posterior. The current flowing through the resistance of the segment would cause by itself a voltage in the opposite sense. Under the action of these two opposing voltages, the net voltage of the anterior end of the segment with respect to the posterior end will be positive or negative as the electromotive force in the segment is greater or less than the voltage drop caused there by the current. Moreover, since the discharge runs along the organ from anterior to posterior, the relation between these two opposing voltages may be different at different instants during the discharge, and the voltage recorded by the oscillograph may change sign, i.e., it may be diphasic. If so, the order in which the two phases occur will be just opposite according to whether it is the electromotive force or the resistance of the electric tissue which varies to produce the discharge. If the electromotive force varies progressively from anterior to posterior while the resistance remains constant, then, before the pulse of electromotive force has reached this segment near the posterior end, the current caused by the electromotive force of the anterior parts will have started in the entire organ and the negative phase of the discharge will be observed in the segment. Only later, when the electromotive force has been generated in the segment and has declined in the anterior parts, will the positive phase occur. On the other hand, if it is the resistance which varies progressively from anterior to posterior, the electromotive force remaining constant, no large current will flow until the resistance of the whole organ, including that of the entire posterior segment, has fallen to a low value. In this case, the voltage across the posterior segment will first become positive, as its cells are thrown into series by the falling resistance, and afterward will become negative, as the impulse reaches the posterior end of the organ, dropping the resistance there and so completing the circuit to allow the passage of a large current. When the observation is made, it is found that the voltage across the segment is first positive, rising sharply for a very brief time, then sharply falling and reversing. Consequently the hypothesis that the discharge is produced by a drop in the internal resistance is favored.
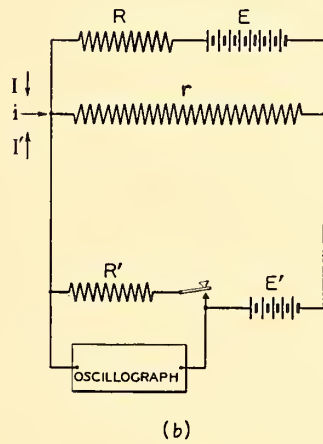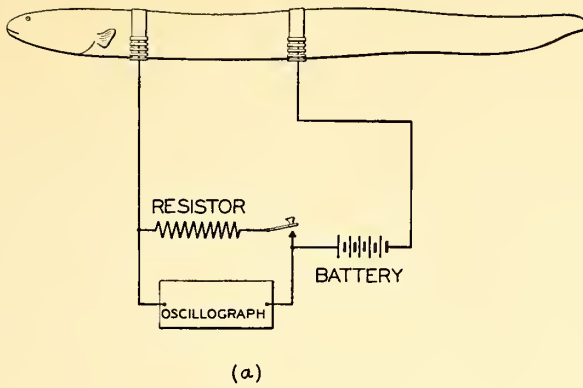
Text-fig. 1.
(a) Electrical connections used in making oscillo-
    graphic traces. (b) The same with a schematic
    representation of the electrical characteristics
    of the eel.

Another evidence of the variation of the internal resistance of the organ during the discharge appears in the oscillographic traces reproduced in Plate I, Figs. 1, 2 and 3. These traces were obtained with electrical connections as shown in Text-fig. 1 (a). The eel was 123 cm. long. The electrodes were in contact with the skin, one 23 cm. from the snout at the anterior end of the large organs, the other 51 cm. from the snout, so that there was included between the electrodes a convenient length of the large organs and necessarily about the same length of Hunter's organs, but none of the organs of Sachs. The electrodes were made of aluminum plates on rubber belts, which were fastened around the eel. They were designed to have an area large enough to avoid a very high current density through the skin. When the eel discharges in the water, the flow of current through the skin is distributed over a large surface. With electrodes of small area in a circuit of low resistance, the high current densities produced in the discharge temporarily bleach and, if continued, seriously injure the skin.

A circuit for the discharge was completed through a resistor and a battery, which could be connected either to reinforce or oppose the discharge of the eel through the resistor. It was necessary in making observations to connect the resistor and battery only briefly in the circuit. The repeated discharge of the eel through a low resistance not only produces the injury to the skin already mentioned but also, of course, exhausts the electric organs. The exhaustion shows itself, at least in eels ·of large size, not in an appreciable reduction of the peak voltage on open circuit but in a reluctance of the eel to discharge. The effects of connection to a battery are more striking. On being connected through a low resistance to a battery of voltage even considerably less than its own and with either polarity of connection, the eel becomes restive. If the connection is maintained, the peak voltage on open circuit declines and the form of the oscillographic trace is markedly altered, the peak becoming much sharper. The alteration persists for some time after the eel is disconnected from the battery. To avoid it in these observations, our procedure was as follows: The eel was made to discharge by gentle prodding. When it was discharging with some regularity, the resistor was thrown into the circuit by a button switch and the camera shutter was opened to photograph the screen of the oscillograph. As soon as traces of the discharge were obtained, the shutter was closed and the button switch released. Since the shutter was always open for the interval of several discharges, the traces of these discharges overlap on the photographs.

In Plate I, Figs. 1, 2 and 3, the resistance was 1,000 ohms. In Fig. 1 the battery voltage was 90 reinforcing the discharge of the eel. In Fig. 2 there was no battery voltage. In Fig. 3 the battery voltage was 90 opposing the discharge of the eel. A constant voltage between the terminals of the oscillograph does not show on the oscillographic trace. If the resistance of the electric tissue were constant during the discharge, the battery would add only a steady voltage to that of the electric tissue. If then the electromotive force of the electric tissue varied during the discharge in the same way for each of the three connections, the same trace would be obtained each time. On the other hand, if the internal resistance of the electric tissue varies during the discharge, the current produced in it by the battery will vary and also the contribution of the battery to the recorded voltage. Thus different traces will be obtained with the three connections. It will be seen that the traces in Plate I are different, the voltage being raised when the battery reinforces the electric organ and lowered when the battery opposes the electric organ. Hence we infer that the resistance varies in the discharge.

In Plate I, Figs. 4 and 5, as in Fig. 2, there was no battery voltage. Plate I, Fig. 4, is the trace of the discharge on open circuit, so that the external resistance was effectively infinite. In Fig. 2 the resistance was 1,000 ohms and in Fig. 5 it was 300 ohms. The current flowing in the organ is increased as the external resistance is lowered, and the drop of the observed peak voltage below the electromotive force is consequently also increased.

Using various battery voltages and external resistances, we have obtained traces of a large number of discharges, and from measurements on these we have undertaken to calculate for different instants during the discharge the values of the internal resistance of the segment of the electric organ employed in the observations, assuming the resistance changing and the electromotive force constant. For this calculation it was necessary to make some assumption concerning the leaking of current through the tissue of the eel adjacent to the electric organ. The paths followed by this current could doubtless be accurately represented in diagram only by a complicated network, but for purposes of rough reckoning we have employed the simple scheme shown in Text fig. 1(b). In this figure, E denotes the elec-

tromotive force of the electric tissue and R its resistance, which we assume changing throughout the discharge. The leakage path is represented by a single resistance r, shunting the electric organ. The electromotive force of the battery is denoted by E′ and the external resistance by R′.

At the junction of the three resistances, the current, I, in the electric tissue unites with the current, I′, in the external part of the circuit to produce the current, i, in the leakage path, and we have:

$$i = I + I'$$

In the circuit comprising E′, R′, and r, there is a drop in voltage I′R′ through the resistance R′ and a drop ir through the resistance r. These must together be equal to the electromotive force E′ of the battery, for around the whole circuit the net drop in voltage must be zero. Hence we have:

$$I'R' + ir = E'$$

Similarly for the circuit comprising E, R, and r, we have:

$$IR + ir = E$$

With these three equations we can eliminate the two currents, I and I′, and obtain for the third current, i, an expression in terms of the electromotive forces and resistances alone. This expression is:

$$i = \frac{ER' + E'R}{RR' + rR + rR'}$$

Except during the discharge, we suppose that R is very large. If this is so, the only appreciable current flowing when the organ is not discharging is that produced by the battery in a circuit closed through the external resistance R′ and the leakage resistance r. If we denote by i_0 the current flowing in r when the organ is not discharging, we have:

$$i_0 = \frac{E'}{r + R'}$$

The voltage between the terminals of the oscillograph is ir − E′ during the discharge and i_0r − E′ between discharges. (The resistance of the battery is low enough that the voltage between its terminals may be regarded as constant and equal to E′.) Hence the variable part of this voltage is ir − i_0r. This is the voltage as recorded on the oscillographic trace. If we denote this voltage by V, we obtain from the two preceding equations:

$$V = r \left\{ \frac{ER' + E'R}{RR' + rR + rR'} - \frac{E'}{R' + r} \right\}$$

Finally, if we solve this last equation for R, we obtain:

$$R = \frac{rR'}{r + R'} \left\{ \frac{E - V}{V} - \frac{E'}{V} \frac{r}{r + R'} \right\}$$

In this expression, E′ and R′ are known, being chosen at will by the connection of different batteries and resistors in the circuit, and V is the voltage measured on the oscillographic trace for any instant during the discharge. E, the electromotive force of the segment of the electric organ, and r, the leakage resistance of the adjacent tissue, are not directly given and values must be sought which will bring into the best possible agreement the values of R calculated for the same instant from different traces. In the calculations E was taken as 260 volts and r as 3,600 ohms.

The values of R calculated from a number of traces obtained with widely varying electrical connections are shown in Text-fig. 2. Each plotted point denotes an average of measurements made on the traces of from four to thirteen discharges. The traces of discharges obtained with the same connections are sometimes rather widely variant. Moreover the measurements could not be made with accuracy, by reason of the lack of high preci-
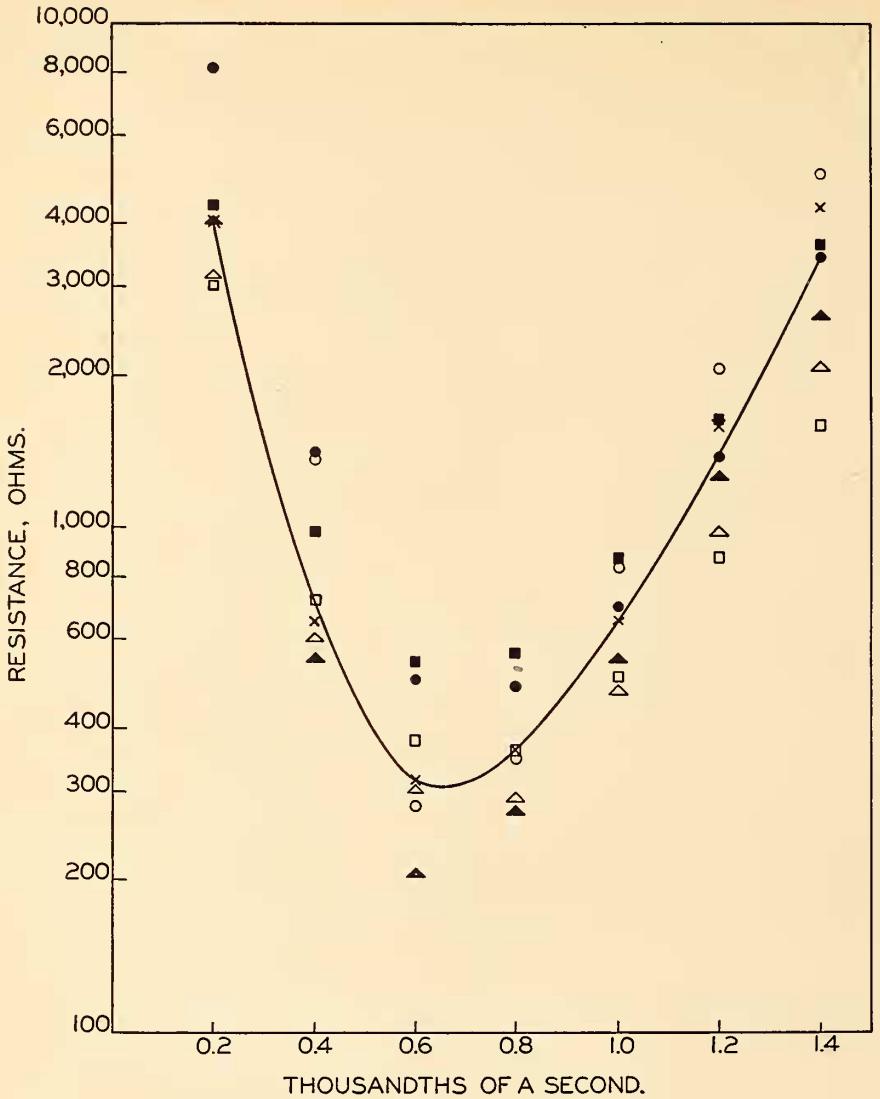
Text-fig. 2.

Resistance of a segment of the large electric organ at different instants during the discharge, calculated from voltages observed when the organ discharges through various circuits.

Open circles ....open circuit
Crosses ....external resistance, 1,000 ohms⎫ No battery
Open triangles .... 300 ohms⎬ voltage.
Open squares .... 100 ohms⎭

Solid circles.....battery voltage, 90 volts reinforcing discharge⎫ External
Solid triangles ....157.5 volts opposing discharge⎬ resistance,
Solid squares ....202.5 volts opposing discharge⎭ 1,000 ohms.

sion of the apparatus and also of the impossibility of finding at all closely on the trace the point corresponding to the instant at which the discharge

began.   It will be observed that the extreme values of the resistance calcu-
lated for any instant during the discharge differ in most cases by a factor
somewhat greater than two.   On the other hand, in the observations from
which the calculations were made, the net electromotive force acting was
varied by a factor of about six and the effective resistance through which
it acted was varied by a factor of about forty.   Considering these wide
variations in the experimental conditions, the inaccuracy of the observa-
tions, and the extreme crudity of the schematic representation in assuming
the leakage current as flowing through a single resistance, we think the
discrepancies in the results are not significant and we consider that the
results confirm the general hypothesis from which the calculations were
made.   Our conclusion is then that the electromotive force of the electric
tissue is almost certainly that of a series of concentration cells, that the
discharge is very probably produced by a transient drop in the internal
resistance of the electric tissue, and that this drop is probably an action of
the nervous impulse at the ends of the nerve fibers which changes a virtual
insulation between adjacent cells into an effective connection.

Two other observations seem worth noting.   One of these is that the
electric tissue is rectifying, that is, during the discharge, when its resis-
tance to an electromotive force in the same direction as its own falls
markedly, its resistance to an electromotive force in the opposite direction
remains high.   As the opposing electromotive force of the battery shown in
Text-fig. 1 is increased, the discharge diminishes in voltage and at a certain
value of the opposing electromotive force disappears altogether.   A further
increase in the opposing electromotive force, up to some 90 volts at least,
produces no additional effect; discharge is not reversed.

The other observation concerns the intermediate discharge.   Since the
major and minor discharges can be definitely attributed to the large organs
and the organs of Sachs, and since the only other electric organs are those
of Hunter, it seems natural to associate the third type of discharge with
these.   However, our observations on the discharge through various resis-
tances indicate that this discharge has a power altogether out of proportion
to the bulk of Hunter's organs.   These organs, while nearly as long as the
large organs, have a very much smaller cross-section.   Consequently their
internal resistance should be much higher and the voltage they could develop
externally across a low resistance should be only a very small fraction of
that developed in the major discharge.   Plate I, Fig. 3, shows one and prob-
ably two intermediate discharges, those of the lowest and next lowest peak
voltages. (They are distinguished from the major discharge by their more
gradual fall as well as by their lower peak voltage.)   The peak voltages of
these two discharges, while definitely lower than those of the major dis-
charges, are still relatively about as large as on open circuit.   Consequently
it would seem that only the large organs would have enough power to pro-
duce the intermediate discharge.   It may be that the intermediate discharge
is a discharge of the large organs modified, in some way of which as yet we
have only a very vague idea, by the simultaneous discharge of Hunter's or-
gans.   On open circuit, the intermediate discharge has sometimes a spur
before the main peak.   This spur may show the discharge of Hunter's
organs.

EXPLANATION OF THE PLATE.

PLATE I.

Oscillographic traces of the major discharge of a segment of the large organ with various electrical connections.

Fig. 1. Battery voltage, 90 volts reinforcing discharge⎤   External
Fig. 2. No battery voltage   ⎬ resistance,
Fig. 3. Battery voltage, 90 volts opposing discharge ⎦ 1,000 ohms.
Fig. 4. Open circuit.
Fig. 5. External resistance 300 ohms, no battery voltage.